EFFECT OF TEMPERATURE ON THE METABOLIC RATE OF SEA URCHINS [1]

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There are several species of sea urchins along the Oregon coast which occupy overlapping but limited vertical ranges. According to Mortensen (1943) the fragile urchin, *Allocentrotus fragilis,* has a bathymetric distribution of about 50–1150 m. Both *Strongylocentrotus franciscanus,* the red urchin, and *Strongylocentrotus purpuratus,* the purple urchin, occur intertidally as well as subtidally. The purple urchin is abundant in the intertidal but also has been dredged from depths as great as 64 m. The distribution of the red urchin is more subtidal than that of the purple urchin and extends from the low tide line to depths of at least 125 m (Mortensen, 1943; Swan, 1953; McCauley and Carey, 1967; Ricketts, Calvin, and Hedgpeth, 1968). The more intertidal species would presumably be exposed to greater thermal variation and show different patterns of metabolic compensation for temperature, compared to subtidal forms.

Although the effect of a variety of factors on the metabolism of sea urchins has been studied—*e.g.,* body size (McPherson, 1968), nutritional state (Farmanfarmaian, 1966), reproductive state (Giese, Farmanfarmaian, Hilden, and Doezema, 1966), oxygen tension (Johansen and Vadas, 1967), salinity (Giese and Farmanfarmaian, 1963), and burrowing (Lewis, 1968)—there are relatively few reports concerning the effect of temperature. Farmanfarmaian and Giese (1963) investigated the metabolic rate-temperature (R-T) relationship in *Strongylocentrotus purpuratus* following temperature acclimation and reported the usual higher metabolic rates in the cold-acclimated forms. In the sea urchin, *Eucidaris tribuloides,* McPherson (1968) has observed higher metabolic rates in winter-acclimatized forms than those of summer at the corresponding temperatures. In this study we examine the metabolic rate-temperature relationships (R-T curves) for summer-acclimatized *S. purpuratus, S. franciscanus,* and *A. fragilis.*

METHODS AND MATERIALS

Definitions and protocols

The terms acclimatization and acclimation are used in this paper according to the definitions of Prosser and Brown (1961). Acclimatization is considered as a naturally occurring physiological compensation to multiple changes in the environment. Acclimation is considered as a compensatory physiological change

resulting from exposure in the laboratory to a single factor, with other environmental factors maintained at as constant a level as possible.

Metabolic rate determinations were carried out over a range of temperatures on animals kept in laboratory tanks for short periods (generally no more than 2–3 days) after collection. These urchins are thus "field-acclimatized."
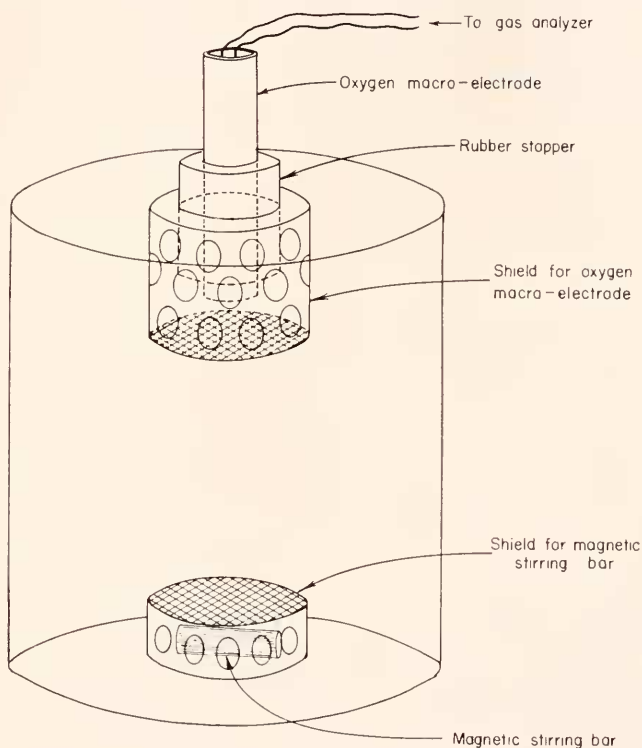

FIGURE 1. Respiratory container.

Collection and maintenance of animals

Purple urchins and red urchins were collected from several different locations on the Oregon coast, over a latitudinal range of 1° 30′. Fragile urchins were dredged with an otter trawl from depths of 150 and 200 m along the oceanographic station line extending directly outwards from Newport, Oregon. Urchins were maintained in aerated, running sea water in fiber-glass holding tanks.

Measurement of oxygen consumption

Oxygen consumption was determined by measuring changes in the oxygen tension of filtered sea water in which the urchin was submerged. The urchin was placed in a closed and sealed "Tupperware" plastic container of suitable size. A variety of sizes was necessary owing to the size ranges of the urchins tested (64.6–177.6 g, 207.7–1658.7 g, and 42.7–115.6 g for the purple, red, and

fragile urchins, respectively). Resulting sea water volumes ranged from 1.72 to 9.20 liters. A magnetic stirring bar was placed at the bottom of each container, and a slow stirring rate, created by an immersible magnetic stirrer (Tri-R Instrument Co.) was used in all studies to provide for uniform temperature and oxygen tension values. A Beckman oxygen macro-electrode was used in conjunction with a physiological gas analyzer (Beckman Spinco model 160) to determine the oxygen tension. Appropriate shields restrained the urchins from interfering with the operation of the stirring bar and the oxygen macro-electrode. The arrangement is pictured in Figure 1.
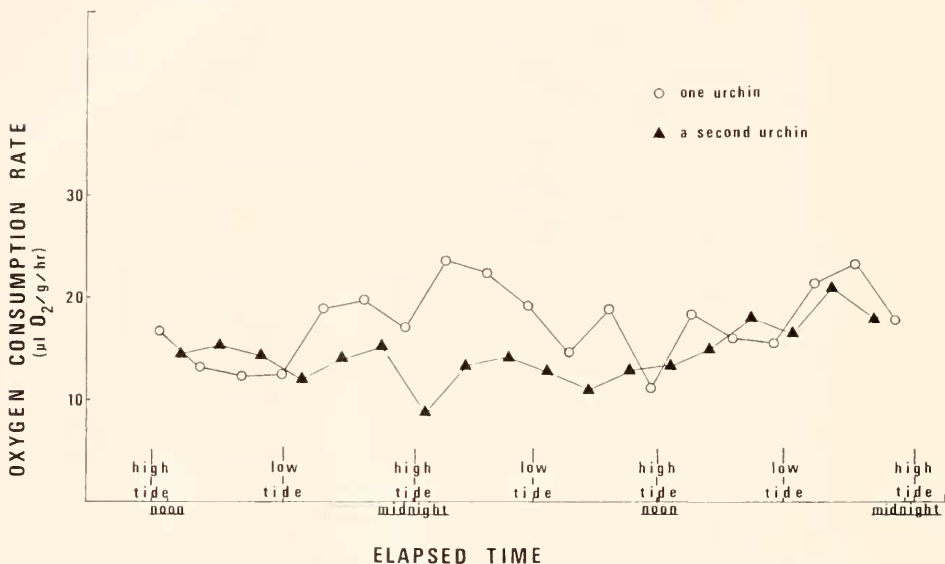

FIGURE 2. Relationship between oxygen consumption rate and elapsed time for *Strongylocentrotus purpuratus*.

The temperature range used was 6° to 24°, with measurements made at 3° intervals. Temperature was maintained with a Bronwill thermoregulator combined with a portable cooling unit (Precision Scientific Company). Urchins were placed in the containers about 5 hrs for equilibration in aerated sea water at 6°, the initial test temperature. The container was sealed and oxygen tension recorded at 10–20 min intervals. In this manner from 3 to 6 measurements of oxygen uptake were obtained. The temperature was then changed to the next level while the respiratory container was aerated. After reaching the new temperature, a one hour period of equilibration was allowed before measurements of oxygen uptake were made. Oxygen tension of the sea water in the container at no time fell below 75 mm Hg, and runs at any one temperature were usually terminated at considerably higher oxygen levels. Measurements of chamber water pH were made from samples taken before urchins were placed in the container, and at the conclusion of testing. Declines of 0.1–0.2 pH unit were observed for initial experiments with urchins. The practice was not continued for the remaining experi-

ments. No effort was made to prevent fouling although no indication of it was observed. All rates are expressed as microliters of oxygen consumed per gram wet weight per hour ($\mu l\ O_2/g/hr$).
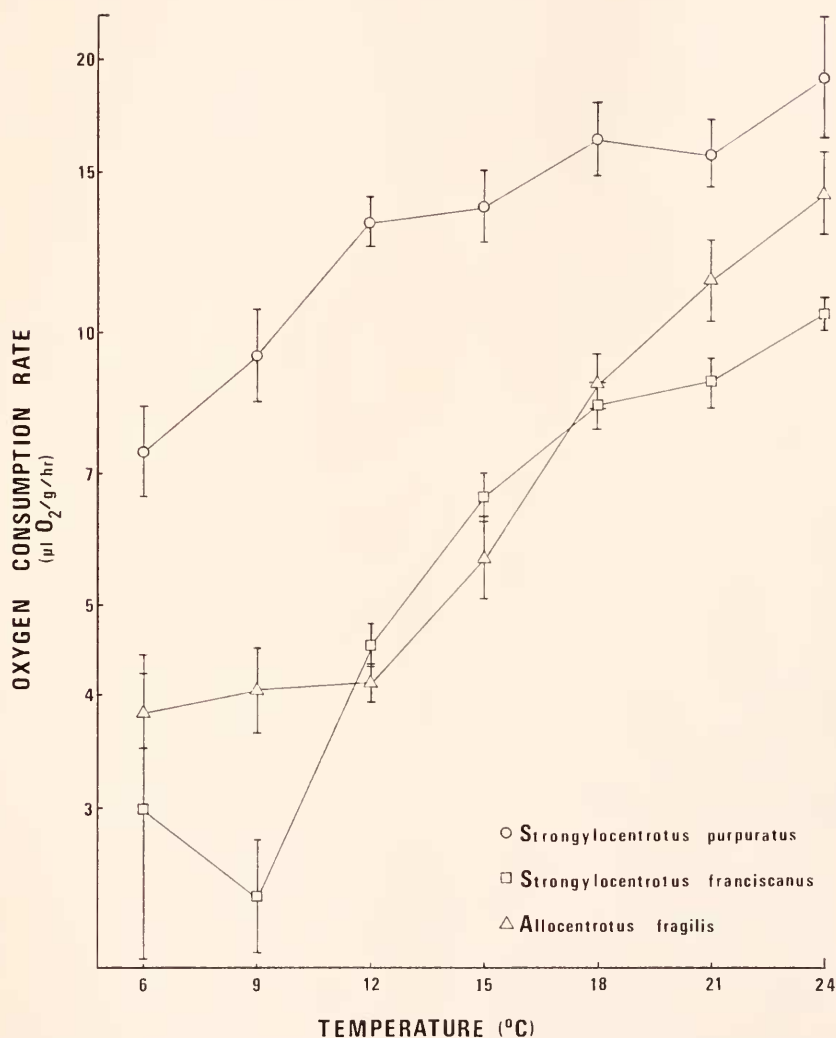

FIGURE 3. Oxygen consumption rate-temperature curves for field-acclimatized sea urchins. Vertical bars indicate 95% confidence limits.

RESULTS

In a preliminary series of tests, the oxygen consumption rates of several individual urchins were determined at frequent intervals for periods greatly exceeding the length of the metabolic rate-temperature experiments. All tests were run at a temperature of 12°. Figure 2, showing the results of a 36 hour experiment—

using two purple urchins concurrently, is representative of the results obtained. There appears to be no clear indication of rhythms in metabolic rate associated with a particular time of day or tidal cycle.

The effect of size upon metabolism is well documented (Zeuthen, 1947, 1953; Hemmingsen, 1960; Prosser and Brown, 1961). McPherson (1968) describes an inverse relationship between metabolic rate and size for the tropical urchin *Eucidaris tribuloides*. Farmanfarmaian (1966) in a review of echinoderm respiratory physiology reports decreasing levels of metabolism with size. In the present study metabolic rates for the purple, red, and fragile urchins are expressed as μl O_2/g/hr corrected to correspond to 97.0, 360.0, and 70.0 g (wet weight) animals, respectively, which constitute approximate mean weights of the test animals. Rates were calculated by determining the linear regression equation for the relation of body size to metabolic rate for all animals under a given set of conditions (species and test temperature). Observation number (n) was 39–42, 22–41, and 13–18 for 12 purple, 12 red, and 6 fragile urchins, respectively. The size-corrected rates are then plotted against temperature in the form of semilog plots (Fig. 3). Vertical bars indicate interval estimates of the population means with 0.95 confidence limits and derive from the following expression (Snedecor and Cochran, 1967):

$$\mu = \hat{Y} \pm t_{0.05} S_{\hat{Y}}$$

where

$$S_{\hat{Y}} = S_{y.x} \sqrt{\left(\frac{1}{N}\right) + \left(\frac{x^2}{\sum x^2}\right)}$$

$$\text{d.f.} = N - 2$$

Figure 3 depicts the metabolic rate-temperature relationships for summer field-acclimatized purple, red, and fragile urchins. Q_{10} values for all temperature intervals are presented in Table I. Rates of the purple urchin rise with temperature from 6° to 12° and 21° to 24° but show considerable rate-temperature independence (Q_{10}'s 0.883 to 1.74) from 12° to 21°. Metabolic rate of the red urchin rises with temperature from 9° to 24°. The mean rate at 6° is higher than at 9°. However, the variability at 6° is greater than at any temperature tested. The rates at both 6° and 9°, moreover, are so low as to be almost

Q_{10} values for oxygen consumption rate-temperature relationships

Temperature range	*Strongylocentrotus purpuratus*	*Strongylocentrotus franciscanus*	*Allocentrotus fragilis*
6°–9°	2.25	0.483	1.22
9°–12°	3.10	8.26	1.07
12°–15°	1.16	3.45	2.82
15°–18°	1.74	2.18	4.47
18°–21°	0.883	1.19	2.35
21°–24°	1.88	1.86	2.11

undetectable. In the fragile urchin oxygen consumption rate appears temperature independent between 6° and 12° and temperature dependent from 12° to 24°.

Other than temperature and body size, factors contributing to variability include availability of oxygen, activity, the nutritional state, and the reproductive state of the animal. In an attempt to minimize the possible influence of reproductive condition (Giese, Farmanfarmaian, Hilden, and Doezema, 1966) all experiments were performed in summer and early fall. At this time the gonads of the intertidal urchins are said to be spent and/or in a state of incipient gametogenesis (Bennett and Giese, 1955; Holland and Giese, 1965; Chatlynne, 1969). In regard to the relation between metabolic rate and oxygen tension, the earlier literature refers to echinoids in general as "conformers" (Hyman, 1929; Farmanfarmaian, 1959, 1966; Prosser and Brown, 1961). Steen (1965) describes a constant level of oxygen consumption for *Strongylocentrotus droebachiensis* at 6° but conformity at 16°. Johansen and Vadas (1967) studied several species of strongylocentrotids and found that oxygen consumption was independent of the ambient oxygen tension down to 60–70 mm Hg, although a close correlation between the oxygen consumption rate and the oxygen tension of the coelomic fluid was noted. In the present study oxygen tension in the respiratory containers never fell below 75 mm Hg.

DISCUSSION

Of the three species used in the study, the purple urchin, *S. purpuratus*, occupies the most exposed habitat and would be expected to encounter considerable fluctuation in temperature during tidal cycles. Gonor (1968) reports a range of 8.5° in the temperature of the surf at Agate Beach during August. Moreover, Gonor (1968) observes that during summer low tides, which occur during daylight hours, the mean internal temperature of purple urchins may rise to as much as 10° above that of the sea surface. Metabolic rate of *S. purpuratus* is essentially independent of temperature between 12° and 21° (Fig. 3). We suggest that the wide temperature range over which rate of oxygen consumption is relatively temperature independent may be adaptive in permitting these animals to maintain constant metabolic rates in the face of considerable temperature variation.

A number of recent studies have reported low Q_{10}'s for a variety of rate functions in many intertidal invertebrates (Baldwin, 1968; Newell and Pye, 1970a, 1970b, 1971). The temperature independence of metabolic rate between 12° and 21° shown by purple urchins in the present study is consistent with these findings. Metabolic rate is temperature dependent below 12° and above 21°.

Although red urchins are found in the lowest reaches of the intertidal habitat, they are for the most part subtidal forms (Mortensen, 1943; Swan, 1953; McCauley and Carey, 1967; Ricketts, Calvin, and Hedgpeth, 1968). Q_{10}'s for metabolic rate of *S. franciscanus* are high at all parts of the test temperature range excepting 6°–9° (Table 1). From 9° to 12°, a range to which this species might reasonably be exposed in nature, an extremely high Q_{10} of 8.26 was found. It would appear that *S. franciscanus*, in contrast to the more intertidal *S. purpuratus*, has a metabolic rate which is essentially temperature dependent.

The fragile urchin, *A. fragilis,* is a deep-water benthic form exposed to a constant low temperature. The annual average bottom temperature measurements from January 1967 to January 1969 at the two stations where the fragile urchin was dredged were $8.20° \pm 0.802$ and $7.58° \pm 0.588$ (A. G. Carey, Jr., Oregon State University, personal communication). The rate-temperature curve for fragile urchins (Fig. 3) shows Q_{10}'s very close to 1.0 from 6° to 12° (Table 1). From 12° to 24° Q_{10}'s are 2.0 or greater, illustrating temperature dependence of metabolic rate. Thus, within the narrow temperature limits to which *A. fragilis* might normally be exposed, it would seem that metabolic rate is maintained at a constant level. It is noteworthy that fragile urchins have much lower rates of oxygen consumption at all test temperatures, compared to purple urchins, even though adults of the two species are similar in size. This may reflect differences in nutrition and/or overall activity of the two species. Paine and Vadas (1969) acknowledge the essentially herbivorous nature of *S. purpuratus,* whereas McCauley and Carey (1967) suggest a detrital form of nutrition for *A. fragilis.*

All three species were tested in summer and early fall, and it is possible that different rate-temperature curves would be found at other times of the year. In the urchin *Eucidaris tribuloides,* for example, McPherson (1968) has observed higher metabolic rates at corresponding temperatures in winter-acclimatized animals compared to summer forms.

SUMMARY

1. The metabolic rate-temperature relationship for several species of sea urchins from different habitats has been determined. Rates were determined over a range of temperatures on animals kept in the laboratory for short periods of time ("field-acclimatized" animals).

2. The benthic *Allocentrotus fragilis* showed rate-temperature independence from 6° to 12°, a range including the habitat temperatures, but dependence (high Q_{10}'s) from 12° to 24°.

3. The relatively subtidal *Strongylocentrotus franciscanus* showed little rate-temperature independence.

4. The more exposed *Strongylocentrotus purpuratus* showed rate-temperature independence over a wide range of temperature (12°–21°).

5. The metabolic rate-temperature results for the field-acclimatized urchins appear to be consistent with the temperature fluctuations of their respective habitats.

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